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Are the Indonesian and western Indian Ocean coelacanths conspecific: a prediction

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Synopsis

It is hypothesized that the ancestor of the extant western Indian Ocean and Indonesian populations of *Latimeria* was continuously distributed along the deeper coasts of massed Africa–Madagascar–Eurasia in early geologic time. The collision of India with Eurasia, roughly 50 MY ago, caused the formation of the Himalayan Mountains and subsequent developement of numerous rivers. The rivers, which flow down both coasts of India, and areas even further east, deposited, and continue to deposit, great amounts of silt along both coasts of India. The siltation destroyed possible coelacanth habitats, thus isolating coelacanth populations to the west of India from those to the east and allowing them to diverge.

Discussion

Coelacanths, presumably conspecific with *Latimeria chalumnae*, have been found recently (September 1997) to occur off Manado, Sulawesi, Indonesia (Erdmann et al. 1998). Previously, the species was believed to be restricted to the southwestern Indian Ocean, some 10 000 km west of Manado. Not in the 60 years since its first reported discovery in 1938, and the subsequent collection of an estimated 200+ specimens, has *L. chalumnae* been reported to occur naturally in waters other than those surrounding the Comoros Islands. Isolated captures off the coasts of Mozambique, southern Madagascar, and South Africa (ca. 800 km SW, 1200 km SE, and 2900 km SW from the Comoros) are considered to be strays transported by the strong prevailing ocean currents in the area (Schliewen et al. 1993). DNA comparisons (Schliewen et al. 1993) of the Mozambique and Comoros specimens indicate that the fish belonged to the same population.

Forey (1998) opined that the Comoro and Sulawesi populations of *Latimeria* are probably 'quite distinct', based on the distances separating them, the different geological histories of the two areas, and the direction of ocean currents in the region. He noted that DNA comparisons between Comoros and Indonesian specimens could test this possibility. If, however, it eventuates that the two populations are undifferentiated, he suggests that the species may be even more widely distributed than currently believed, and much more deeply occurring, thus enabling the species to transcend the great ocean depths necessary for it to have dispersed to Indonesia (or vice versa). I concur with Forey in predicting that molecular (and/or morphological) evidence will show that the two populations are distinct. The following discussion develops my reasons.

Information on reproductive mode, ecology, age, population structure, food, and behavior of the Indian Ocean population of *Latimeria chalumnae* have been summarized by Wourms et al. (1991), Bruton & Stobbs (1991), Bruton & Armstrong (1991), Fricke et al.

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(1991), Uyeno (1991), and Uyeno & Tsutsumi (1991). *Latimeria chalumnae* is a large (to 1.8 m total length), live bearer, producing 'enormous' eggs and relatively few (up 26; Bruton et al. 1992), large young, with a population size in the Comoros estimated to comprise fewer than 500 individuals.

The largest late-term embryo recorded is 358 mm total length (Bruton et al. 1992) and the smallest free-living specimen available, a neonate, is 420 mm; however, a native fisherman reported seeing a 250 mm specimen with completely resorbed yolksac swimming in apparent distress near the ocean's surface. The age attained by available specimens, based on scale readings, is either 11 or 22 years, depending on whether annuli are produced at the rate of one or two per year. Native fishermen in the Comoros have reported coelacanth catches from depths of 40–1000 m, but observations to depths over 300 m made from submersibles indicated that the species is limited to depths no greater than 253 m, which is roughly the depth limit of rocky caves in the area. Coelacanths are bottom or epibenthic drift feeders, that remain inactive in deep caves during the day, but ascend to shallower depths at night, apparently to feed. They appear to be slow swimmers, but capable of quick motions of short duration. They are confined mostly to waters with temperatures below 18°C, although water temperatures in the caves they entered approached 23°C.

The information recounted might be expected to be descriptive of a fish with a restricted distribution. A relatively large, deep-water, epibenthically associated, cave-dwelling fish without a planktonic larva, and with low fecundity and population density is an unlikely candidate for successful long-distance dispersal by currents. Bruton & Stobbs (1991), however, may be correct in suggesting that the distribution of coelacanth populations may be wider than just the Comoros in the western Indian Ocean. In this respect, they cite particularly the eastern coasts of Madagascar, northern Zululand, and the southeast coast of South Africa, which have deep rocky reefs and have not been explored with the appropriate fishing gear. If they are correct, the South African waif, noted earlier, could have well been a resident of that coast. Certainly, if the distribution patterns of shallow-dwelling (to ca. 30 m) shore fishes restricted to the western Indian Ocean are an indication, *Latimeria* is probably more widely distributed in the area than is currently indicated.

Gordon (1998) has taken issue with Forey's (1998) assertion that ocean currents in the Indian Ocean would support the distinctiveness of the Comoros and Indonesian coelacanths. As cited by Gordon, Gordon (1986), Gordon & Fine (1996) and Gordon et al. (1997) have shown that 'there is a direct flow of surface and thermocline (upper 400 m) water from the Mindanao Current . . . into the Sulawesi Sea. After transversing Makassar Strait this flow, called the Indonesian Throughflow, enters the Flores and Banda seas before spreading into Timor Sea and Indian Ocean. Once in the Indian Ocean the Indonesian water spreads westward . . . embedded within the South Equatorial Current along 12° S, eventually reaching the Comoran Islands.' Gordon concluded that coelacanth populations might exist along the route of this flow.

The average surface velocity of the westward flowing South Equatorial Current (SEC) is about 24 nautical miles per day (A.L. Gordon personal communication). At 10–15° S, it would take an object in the current about 175 ± 25 days to make the transit from 120° E, approximate longitude of entry of Indonesian flowthrough water into the Indian Ocean (Gordon & Fine 1996, Gordon et al. 1997) to 50° E, longitude of NE Madagascar, first major landfall of the SEC in the SW Indian Ocean. Christmas (106° E) and Cocos-Keeling (97° E) islands in the eastern Indian Ocean lie within the current and could possibly harbor coelacanths, thus decreasing the transit time. It seems doubtful, however, that a coelacanth caught in the SEC could make the transit to landfall in the western Indian Ocean in less than 100 days. That a bottom dwelling fish could prevail for 100 or more days in the open ocean is problematic.

Mauritius, Seychelles, and Maldive islands in the western Indian Ocean would seem to be likely candidates for harboring coelacanths, but because of heavy fishing in these areas and the presence of knowledgeable residents (variously including ichthyologists), if coelacanths existed in or strayed into these areas they would have been caught and recognized by now. The coasts of India are washed by silt-laden waters caused by the numerous rivers emptying along the coasts and, therefore, would not be expected to harbor coelacanths.

If the coelacanth populations in the western Indian Ocean and Indonesia prove recognizably different, as I predict, the geological history of the area, as Forey noted, but did not describe, may provide an explanation of how the divergence was initiated. For this, I propose the following abbreviated scenario.

At some earlier time, the ancestor of the present coelacanth populations must have had a more-or-less

continuous distribution that was interrupted later by a barrier. During the late Jurassic (ca. 140 Mya), just prior to the beginning of the breakup of the southern continents (Audley-Charles et al. 1981, figure 3.3), Africa, Madagascar, Antarctica, and Australia were united, and Africa was linked northwards with the Eurasian plate. The distribution of ancestral *Latimeria* was more-or-less continuous along the coasts of these massed continental blocks. India separated from Madagascar and began its move north in early Cretaceous (140–120 Mya; Audley-Charles et al. 1981, figure 3.4), possibly carrying coelacanths with it. Madagascar separated from Africa shortly thereafter, but its separation ceased by magnetic anomaly 2 (ca. 115 Mya; Besse & Courtillot 1988; however, Rabinowitz et al. 1983, propose that Madagascar began separating from Africa about 180 Mya and ceased at 120 Mya). India continued its 'flight' north and began colliding with the Eurasian plate in Eocene (40–50 Mya; Audley-Charles et al. 1981, figure 3.8). Continuous and still continuing movement of India into the Eurasian plate caused the building of the Himalayan Mountains, which resulted in the formation of many great rivers that flooded into the Indian Ocean down both coasts of India and the coast of Burma; e.g., the Indus, Ganges, and the Ayeyerwady (Irawaddy). The heavy siltation covered the bottom, both near shore and deeply offshore, and eliminated habitats suitable for *Latimeria*. India, thus formed a barrier between coelacanth populations to the east (Africa–Madagascar) and west (Malaysia–Indonesia; see color maps for 30 Mya in Hall 1997).

The isolation of the Comores and Indonesian coelacanth populations probably began several million years after the docking of India with Eurasia. The formation of the Himalayas and associated major river systems would have taken considerable time to develop. According to Gansser (1964) a major river system, forerunner of the Indus (and possibly the Ganges), was not developed until the Siwalik epoch (Middle Miocene, which would be about 15 Mya).

Hocutt (1987) first proposed that the movement of India north and its junction with the Eurasian plate was the vicariant event that explains a relatively high rate of endemism in marine organisms in the western Indian Ocean. Springer & Williams (1990) reported that many fishes and other marine organisms are represented by disjunct populations or sister groups in the Indian and Pacific oceans. Although these circumstances have been reported to apply only to shallow-dwelling organisms, and in the case of Springer & Williams (op. cit.), believed to be the product of glacial sea-level changes, the distribution patterns may apply to deeper-dwelling organisms as well.

In summary, I believe the collision of India with the Eurasian plate formed a barrier isolating the distributions of many marine organisms, including coelacanths, in the western Indian Ocean from those in the eastern Indian Ocean and/or Pacific Ocean, thus allowing the populations on either side of the barrier to diverge.

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